The taxonomic status of the genera *Pontigulasia*, *Lagenodifflugia* and *Zivkovicia* (Rhizopoda: Difflugiidae)

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Introduction

The significance of the different structural elements utilised to provide an internal dividing wall in the shell of the genus *Pontigulasia* Rhumbler, 1896 was employed by Ogden (1983) to divide the genus into two, with the creation of a new genus *Zivkovicia* Ogden, 1983. At the same time a new genus *Lagenodifflugia* was erected by Medioli & Scott (1983) to accommodate *Difflugia vas* Leidy, 1874, a species that he (Leidy, 1879) later redescribed as a variety of *Difflugia pyriformis*. Medioli & Scott (1983) considered their new genus to be distinct from species of *Difflugia* because the shell was divided into a bulbous main part and a neck, the two parts being separated by an internal diaphragm pierced by a single, central, usually large orifice. In the same work Medioli & Scott redefined the genus *Pontigulasia*, describing the main characters as a constriction of the neck marking the position where a perforated internal diaphragm often extends across this region, and at times a bent neck combined with the internal restriction simulating a spiral arrangement. They also stated that the diaphragm is seldom present in fossilised forms. The amendment of the diagnosis to contain a 'bent neck' was made to allow Medioli & Scott to include some '*Lecquereusia*-like' specimens in their description of *Pontigulasia compressa*, and to suggest the possibility of combining the genera *Lesquereusia* and *Pontigulasia*, the former being the senior synonym.

I am most grateful to Dr Drew Haman and Dr Georges Merinfeld for directing my attention to the nomenclature problems posed by the creation of these two new genera. The present report is an attempt to clarify the status and diagnosis of the three genera *Pontigulasia*, *Lagenodifflugia* and *Zivkovicia*.

Taxonomy

The taxonomic problem caused by the creation of two new genera relates to the interpretation and validity of the structures and openings found associated with the inner dividing wall. There are only a few descriptions and figures of these features around which the diagnoses have been erected. One reason for this is the difficulty of trying to see inside the shell either *en face* or laterally due mainly to the opacity of the mineral particles of which it is constructed. Several techniques have been tried to overcome this, for example immersion in clove oil or canada balsam and demineralisation by hydrofluoric acid. Modern techniques have now obviated this problem and allow a new appraisal of this feature (Ogden, 1983).

Each genus will be reassessed here on the basis of the available descriptions and the author's earlier observations.

Pontigulasia Rhumbler, 1896

The first author to recognise the inner dividing wall was Rhumbler (1896) who erected the genus *Pontigulasia* using this feature as a major diagnostic character to separate it from *Difflugia*, and described and clearly figured it as an internal 'schlundbrücke'-throat bridge. He described three

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new species belonging to this genus, *P. compressa, P. incisa* and *P. spiralis*. Since then Hopkinson (1919) has redescribed *P. compressa* under a new name *P. rhumbleri,* the name *compressa* was preoccupied by Carter's (1864) species, and *P. incisa* has become a synonym of *P. elisa* (Penard, 1893), both the earlier descriptions being for species of *Difflugia*. The authoritative date for *P. rhumbleri* is considered to be Hopkinson's redescription (1919), not the note mentioned as an addition to *P. elisa* on p. 162 of Cash & Hopkinson (1909) where Hopkinson suggests that 'Rhumbler's *P. compressa* (which might now be called *P. Rhumbleri*)', his brackets. Furthermore, the date of Rhumbler's work is erroneously quoted by Cash *et al.* (1919) and Loeblich & Tappan (1964) as 1895, which is the date of presentation, whereas the publication date of the volume was 1896, as listed in Penard's (1902) bibliography.

The internal bridge has been redescribed by Ogden (1983), who examined the dividing wall *in situ* using scanning electron microscopy, and showed it to be correctly termed a bridge, as it represented a rather weak connection between the two lateral walls of the compressed shell in *P. rhumbleri*. It is often difficult to see by optical microscopy because the shells are laterally compressed, and in this the normal viewing position the bridge appears to be a dark floating band situated centrally in the neck region without any apparent connection to the shell wall. This is not surprising, because each junction of the bridge with the wall is about a sixth of the shell diameter at this point.

Although Rhumbler described three species, since that time two of these *P. incisa* and *P. spiralis* have been considered to be synonyms (Cash & Hopkinson, 1909), and it was not until Leoblich & Tappan (1964) that a type species, *P. rhumbleri,* was designated.

DIAGNOSIS. Shell pyriform, sometimes with a constriction of the neck, either circular or compressed in transverse section; composed mainly of agglutinate mineral particles with some diatom frustules or siliceous plates, bound by a network of organic cement; aperture terminal, circular; internally the shell is divided into two regions by a narrow bridge, made mainly of organic cement with some agglutinate particles, stretched between the lateral walls at about one third of the body length from the aperture. Type species *P. rhumbleri* Hopkinson, 1919, with four other species (Chardez, 1985), *P. compressoidea* Jung, 1942; *P. elisa* (Penard, 1893); *P. sarrazinensis* Chardez & Gaspar, 1984 and *P. spiralis* Rhumbler, 1896.

Lagenodifflugia Medioli & Scott, 1983

This genus was established for the single species *Difflugia vas* Leidy, 1874. After his original description Leidy later considered (1879) that this species was a variety of *Difflugia pyriformis,* from which it differed by a constriction of the neck, there was no reference to an internal structure associated with the constriction. Penard (1902) transferred this species to *Pontigulasia* and considered it to be a synonym of his new species *P. spectabilis*. It was corrected to the valid binomen *P. vas* by Schoutenden (1906), and *spectabilis* has since been considered a synonym of *vas*. As *P. vas* was described as having a similar external constriction to *spectabilis,* the assumption was that it had two openings bisecting the internal diaphragm. Notwithstanding this, Stump (1935, 1936 and 1943) in a series of experiments with specimens he initially thought were *Difflugia oblonga,* later found that in sectioned shells there was an internal division with a single opening and subsequently described them as *Pontigulasia vas*. Although Stump does not clearly state that his specimens had a single, central opening, his diagrams without exception suggest that this interpretation is correct. That the strength of the diaphragm is equal to that of the shell wall is extrapolated from his de-mineralised sections which show the continuous nature of these structures.

Using the joint reports of Leidy and Stump, a composite description of a species emerges: it sometimes has a constriction of the neck that separates the anterior third of the shell from the main body; at this point an internal diaphragm is present which is pierced by a single, central, circular opening.

Medioli & Scott (1983) do not illustrate the internal division in their specimens but describe it as a 'large orifice'. They presume that their material is conspecific with that of Leidy and Stump, possibly because all the specimens were collected in America. Fortunately, a single specimen with an internal division was found in material kindly left at the British Museum (Natural History) by F. S. Medioli and helps to confirm their presumption. The specimen had the following measurements: 174 μm long, 108 μm broad, diameter of aperture 37 μm and diameter of internal opening 27 μm. Furthermore the organic cement pattern of this specimen was typical of that illustrated earlier (Ogden, 1983).

DIAGNOSIS. Shell pyriform, often with a constriction of the neck, most frequently circular in cross-section but sometimes slightly compressed, composed mainly of agglutinate mineral particles bound by an organic cement; aperture terminal, circular; internally the shell is partitioned into two regions by a diaphragm constructed as part of the shell wall but having a single central orifice. Type species *L. vas* (Leidy, 1874). Three other species are here attributed to the genus on the basis of having a single opening in a well constructed diaphragm: *L. bryophila* (Penard, 1902) (see Ogden, 1983 for recent description of this species); *L. montana* (Ogden & Zivkovic, 1983) and *L. epiouxi* (Chardez & Gaspar, 1984).

Zivkovicia Ogden, 1987 gen. nov.

This genus was erected by Ogden (1983) to accommodate those species of *Pontigulasia* which had a diaphragm with either one or two internal openings. At that time no distinction was drawn between the number of openings in the diaphragm. With the creation of *Lagenodifflugia* to represent those specimens with a single opening, *Zivkovicia* is redefined here to represent those species with two openings.

In the earlier report (Ogden, 1983), due to an oversight, a type species for *Zivkovicia* was not designated, so under Article 13(b) of the International Code of Zoological Nomenclature the genus is not taxonomically valid. Nevertheless, the name is still available and to avoid confusion is used again here, with an amended diagnosis.

Although Carter's (1864) original description of *Diffugia compressa* did not include a mention of an internal diaphragm, his drawings are so precise that they show the typical V-shaped notch on the shell which represents the internal diaphragm. This structure is clearly illustrated by Figs 18–25 of Ogden (1983). It is therefore proposed as the type-species of the genus. The earlier discussion (p. 14) relating to the incorrect synonymy of *P. vas* and *P. spectabilis,* allows *spectabilis* to be available to include the original description of specimens with a bisected diaphragm (Penard, 1902) and the recent description by Ogden (1983), whose *P. vas* now becomes a synonym of *Z. spectabilis.*

DIAGNOSIS. Shell pyriform, often with a distinct constriction of the neck region, either circular or compressed in transverse-section, composed mainly of agglutinate mineral particles bound by an organic cement matrix; aperture terminal, usually circular; internally the shell is partitioned into two parts by an extension of the shell wall to form a diaphragm which is bisected by two circular openings. Type species *Z. compressa* (Carter, 1864), other species *Z. spectabilis* (Penard, 1902) and *Z. flexa* (Cash & Hopkinson, 1909). A recent description of the latter species can be found in Ogden (1983).

Discussion

Associated problems of clearly identifying the internal openings were discussed previously (Ogden, 1983). Suffice to say here that both these openings and the aperture can be sealed by an organic cyst membrane, and the incidence of a single specimen with a trisected diaphragm in *Z. compressa* (Fig. 28, Ogden, 1983) is considered to be an isolated deformity.

In discussing a possible relationship between *Pontigulasia* Rhumbler, 1896 and *Lesquereusia* Schlumberger, 1845, Medioli & Scott (1983) suggest that both genera are characterised by a constriction at the base of the neck which corresponds to an internal diaphragm, and further state that a morphological intergradation exists between the two genera. They consider that the remaining difference between the genera, that *Lesquereusia* is constructed of siliceous idiosomes whereas *Pontigulasia* is always reported to be composed of xenosomes, is insufficient to separate these two genera.

It has already been established by Stump (1936, 1943) that *P. vas* would not construct a shell or reproduce in the absence of extraneous material, even in the presence of abundant food, and that such deprived animals commenced normal reproductive activities when shell making material was reintroduced. He concluded that *P. vas* was unable to secrete its own shell material and suggested a possible alternative that individuals might be produced without a shell covering. No reports of such naked individuals have been recorded in the literature, but it is well known that some agglutinate species are capable of constructing an organic shell, identical to that which in the field incorporates mineral particles (Hedley *et al.*, 1976; Netzel, 1972, 1976). Furthermore, the deposition of siliceous structures by *Lesquereusia spiralis* are carried out in the cytoplasm of the animal (Harrison *et al.*, 1981), and this species is capable of constructing a shell in the absence of extraneous material. It is equally capable of incorporating xenosomes and Stump used this ability for creating 'windows' to observe cytoplasmic activity. A new family the Lesquereusiidae was designated (Ogden, 1979) to include those members of the Lobosia which secrete their own siliceous elements, e.g. *Lesquereusia, Netzelia* Ogden, 1979, and *Quadrulella* Cockerell, 1909.

The suggestion by Medioli & Scott (1983) of considering a relationship between *Lesquereusia* and *Pontigulasia* is perhaps best treated as an indiscretion on the part of geologists venturing into the alien field of biology. Phylogenetic interpretations should be based on the animal as a complete organism, which in protozoa would include information on cytoplasmic detail, movement, reproduction as well as external coverings, especially when such information exists in publication and the animals are easily collected from the field.

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Since this manuscript was submitted for publication the author has become aware of a paper by Medioli & Scott (1985), in which they have designated type specimens for certain species. In dealing with species of *Pontigulasia, Lagenodifflugia* and *Zivkovicia* they make assumptions based solely on published descriptions and micrographs of fossil specimens, which do not have information relating to the main diagnostic feature the internal dividing diaphragm. In their original paper (Medioli & Scott, 1983), they comment on never having been able to satisfactorily observe the diaphragm of *P. compressa* (Carter, 1864), and their failure is again reiterated in Medioli & Scott (1985), As neither their figures nor plates illustrate an internal structure it suggests that they have failed by both optical and electron microscopy to see this feature in any of their specimens. They presume the presence of a diaphragm solely on it corresponding in position to the external constriction. Although they admit that this external constriction is often obscured by agglutinate material.

Furthermore, the specimen they selected as neotype of *L. vas,* from their Maritime Canada sample does not even resemble the original selected figure from Leidy (1879). In fact they chose an example which was intermediate between Leidy's figured specimen, a smoothly agglutinate form, and their extreme cases of coarse agglutination.

Both of Medioli & Scott's (1983, 1985) papers concerning these genera must be of minimal value because of their failure to describe or identify the internal structures which typify these genera. Its absence suggests that they have been examining species of *Difflugia.* Their insistance that the diaphragm is absent in fossil forms (p. 35, 1983; p. 29, 1985) of *Pontigulasia compressa* (Carter, 1864) would indicate that they are dealing with species of *Difflugia.* The construction of the diaphragm in this species (Ogden, 1983) is so robust, being continuous and as thick as the shell wall, that even in fractured shells it is the wall that breaks and not the diaphragm. Although often by convenience such breaks occur at the junction of the wall and diaphragm. Notwithstanding this, specimens clearly identified as *Zivkovicia compressa* (Carter, 1864) have been recovered from core samples taken in Lake Ullswater which had complete diaphragms (Ogden & Ellison, in prep.), and in addition possessed the typical organic cement units, described by Ogden (1983), specific to this genus.

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